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INLAND-WATER CALANOID COPEPODS OF KANGAROO, KING AND FLINDERS ISLANDS: BIOGEOGRAPHY AND ECOLOGY

by I. A. E. BAYLY*

Summary

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Calanoid copepod identifications are provided for samples from 16 localities on Kangaroo Island, 18 on King Island and 11 on Flinders Island. The number of species found was five, three and seven, respectively. Conductivity data are given for most localities. Species richness in relation to land area is tabulated and discussed. *Boeckella major* is recorded from South Australian territory for the first time. The occurrence of *Hemiboeckella searli* in temporary pools and amongst dense macrophytes in lakes may be due to the absence of predators in young pools and the difficulty encountered by predators in searching dense weed-beds in lakes. The disjunct distribution of *Calamoecia gibbosa* is explicable on the basis of east to west dispersal along a lowland plain during the Pleistocene when sea levels were low, followed by marine inundation.

KEY WORDS: Copepoda, Calanoida, biogeography, ecology.

Introduction

Following the glacial (and aridity) maximum that occurred in the Late Pleistocene at about 18 ka B.P., deglaciation, and the consequent rise in sea level (Chappell 1978; Galloway & Kemp 1981), converted several areas of land along the southern margin of the Australian continent into islands. The nature and fate of the samples of the fauna of greater Australia provided by these islands is a matter of considerable interest. Rawlinson (1974) studied this issue with reference to the reptiles of Bass Strait islands and Tasmania and showed that a whole series of islands in Bass Strait and off South Australia became isolated during the period 16.5 - 6.3 ka B.P.

Despite their small size and the ability of many of them to produce desiccation-resistant eggs, freshwater calanoid copepods are widely acknowledged to exhibit poor dispersal ability (Bayly & Maly 1991; Bănărescu 1990; Bayly 1995). As a consequence, the biogeography of calanoid copepods is of considerable interest, with dispersal playing a smaller role than has been supposed by the numerous workers who simplistically equate the possession of resting eggs with good powers of dispersal (Bayly & Morton 1978).

This paper aims to examine the relationship of the calanoid fauna of three offshore islands (Fig. 1) with that of mainland Australia and Tasmania and to consider the role of historical and ecological factors in observed differences and similarities.

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Methods

Each body of water was thoroughly sampled with a zooplankton net of mesh size 150 μm. Collections were preserved in 10% formalin. Conductivity of a water sample taken from the field in a polyethylene bottle was determined in the laboratory with a Radiometer CDM2e conductivity meter. Where the K_{25} exceeded 5.0 mS cm^{-1}, the conductivity value was converted to a salinity value using the method of Williams (1986). For the King Island localities, pH was measured with a Metrohm E599 portable pH-meter.

With two exceptions, the Flinders Island localities were sampled by the author alone at various times between 1985 – 1988, and by the author working with a limnological team from 10-12 February 1993. The King Island samples, with one exception, were taken by a team of workers including the author during the period 2 -5 December 1991. With two exceptions, the Kangaroo Island samples were collected by the author alone during the period 26 June - 3 July 1994.

Results

Physico-chemical and biological results are summarised in Tables 1 - 3. Five calanoid species were recorded from Kangaroo Island, with only two species, *Boeckella triarticulata* and *Calamoecia clitellata*, occurring at those localities with a salinity of 3.3 g l^{-1} or more. At the less saline localities, *B. major* was restricted to temporary waters. Only three species were found on King Island, and one of these, *B. pseudochelae*, occurred in the sole temporary water body that was sampled. *C. tasmanica* was the only species found in waters with a recorded pH of less than 6.0. None of the King Island waters included in the survey was saline. Seven species were recorded from Flinders Island with *C. tasmanica* most common. *B. symmetrica* was the only species common to all three islands.

TABLE 1. *Occurrence of calanoid copepods on Kangaroo Island.*

Locality	Sampling date	Permanency[a]	Conductivity $[K_{25}]$ (mS cm^{-1})	Salinity (g l^{-1})	Species[b] Bm	Bs	Bt	Ca	Cc
Dam 1 near Penneshaw[c]	20.viii.1991	P				x		x	
Dam 2 near Penneshaw[c]	20.viii.1991	P				x			
Waterhole edge Edwards Lagoon	30.vi.1994	T	0.21		x				
Pond Roper Road	1.vii.1994	T	0.22		x	x			
Lake at Karatta	28.vi.1994	SP	0.31			x		x	
Pond nr rush Lagoon	27.vi.1994	T	0.44		x				
Pond south end Roper Road	1.vii.1994	SP	1.23			x			
Ditch east Kingscote Airport	27.vi.1994	T	1.71		x	x			
Small Grassdale Lagoon	28.vi.1994	SP	3.00			x			
Big Grassdale Lagoon	28.vi.1994	P	3.65			x			
Kaiwarra Cottage Pond	2.vii.1994	T	5.8	3.2	x	x			
Duck Lagoon	1.vii.1994	P	6.0	3.3			x		
Discovery Lagoon	27.vi.1994	T	9.0	5.1			x		
Lake Ada	3.vii.1994	P	12.8	7.5			x		
Murray Lagoon	3.vii.1994	P	15.3	9.1			x		
White Lagoon	27.vi.1994	SP	75.3	51.3					x

a. P = permanent; SP = semi-permanent; T = temporary
b. Bm - *Boeckella major* Searle; Bs = *B. symmetrica* Sars; Bt = *B. triarticulata* (Thomson); Ca = *Calamoecia ampulla* (Searle); Cc = *C. clitellata* Bayly.
c. collected by N. Frick

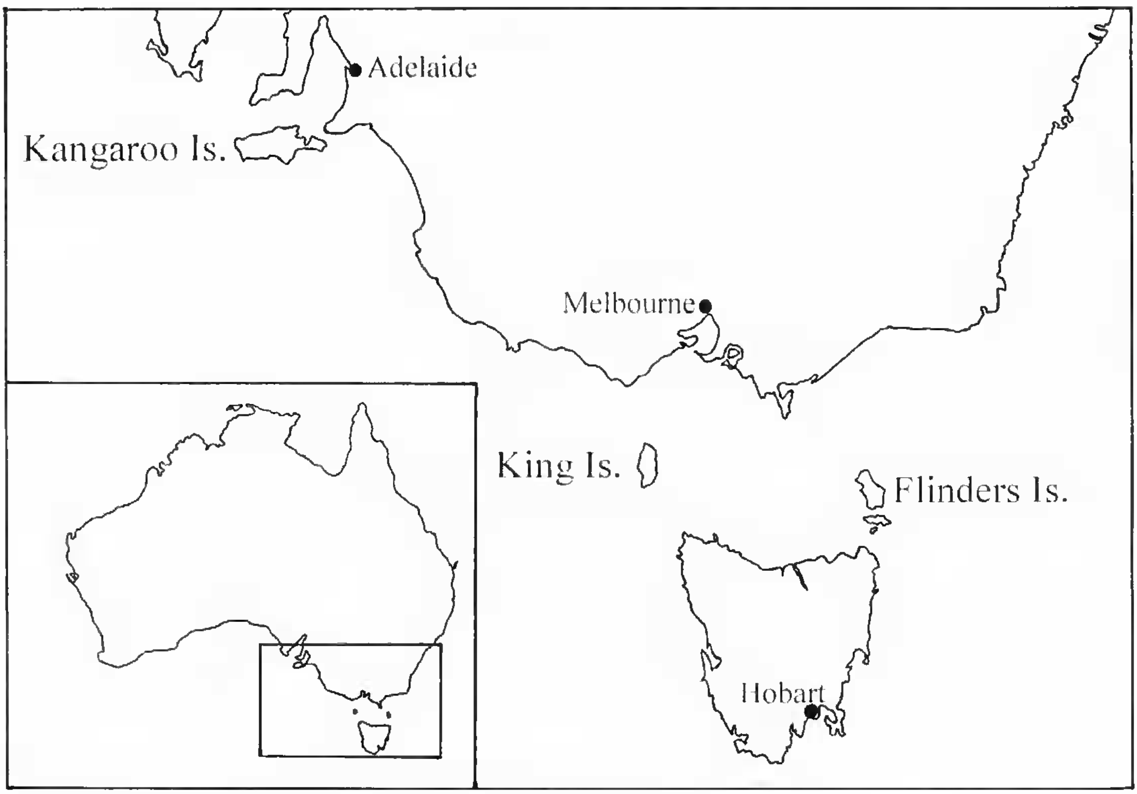

Fig. 1. Map showing location of Kangaroo, King and Flinders Islands.

TABLE 2. *Occurrence of calanoid copepods on King Island.*

Locality	Sampling date	Permanency[a]	Conductivity $[K_{25}]$ (mS cm^{-1})	pH	Species[b] Bp	Bs	Ct
Pool nr Currie[c]	8.xi.1963	T	-	-	x		
Meatsafe Lagoon	5.xii.1991	P	0.56	3.8			x
Dead Sea	2.xii.1991	P	0.56	4.7			x
Lake Martha Lavinia	3.xii.1991	P	0.75	5.2			x
Seal Rock Lagoon (North)	4.xii.1991	P	0.96	7.9		x	
Pearshape Lagoon	2.xii.1991	P	1.04	7.8		x	
Lake nr Surprise Bay Homestead	4.xii.1991	SP	1.10	7.4		x	
Lake opp. Pearshape Lagoon	2.xii.1991	P	1.13	8.2		x	
Pennys Lagoon	3.xii.1991	P	1.15	7.7		x	x
Granite Lagoon	5.xii.1991	P	1.26	6.4		x	
Pioneer Lagoon	4.xii.1991	P	1.46	7.8		x	
Lake btn Denbys & Pioneer Lagoon	2.xii.1991	P	1.47	7.2		x	
Denbys Lagoon	2.xii.1991	P	1.57	6.6		x	x
Lake east end Pioneer Lagoon	4.xii.1991	SP	1.80	8.5		x	
Seal Rock Lagoon (Middle)	4.xii.1991	SP	1.90	7.5		x	x
Cask Lake	3.xii.1991	P	1.96	8.2		x	
Lake Wickham	3.xii.1991	SP	2.15	8.9		x	
Lake Flannigan	3.xii.1991	SP	2.28	9.9		x	

a. P = permanent; SP = semi-permanent; T = temporary
b. Bp - *Boeckella pseudochelae* Searle; Bs = *B. symmetrica* Sars; Ct = *Calamoecia tasmanica* (Smith);
c. collected by M. J. Littlejohn.

TABLE 3. *Occurrence of calanoid copepods on Flinders Island.*

Locality	Sampling date	Permanency[a]	Conductivity $[K_{25}]$ (mS cm^{-1})	Salinity (g l^{-1})	Species[b] Bm	Bp	Bs	Bt	Hs	Cg	Ct
Brodies Lagoon[c]	May 1962	T						x			
Scotts Lagoon[c]	May 1962	T								x	
Pond nr Sticks Lagoon	15.v.1985	T									x
Pond (1) nr Killiecrankie	5.vi.1988	T			x						
Pond (2) nr Killiecrankie	5.vi.1988	T					x				
Reedy Lagoon	9.vi.1988	P				x				x	
Shag Lagoon	12.ii.1993	T	1.7								x
Lake btn N & S Patriarchs	19.v.1985	SP	2.2						x		x
Small lake (1) nr Singleton's Lagoon	10.ii.1993	T	2.4								x
Small lake (2) nr Singleton's Lagoon	10.ii.1993	T	5.1	2.7							x
Sticks Lagoon	15.v.1985	T	12.3	7.1				x			

a. P = permanent; SP = semi-permanent; T = temporary
b. Bm - *Boeckella major* Searle; Bp = *B. propinqua* Sars; Bs = *B. symmetrica* Sars; Bt = *B. triarticulata* (Thomson); Hs = *Hemiboeckella searli* Sars; Cg = *Calamoecia gibbosa* (Brehm); Ct = *C. tasmanica* (Smith).
c. collected by W. D. Williams

Discussion

It is probably not valid on the basis of Tables 1-3 to attempt straightforward and unqualified comparisons between the faunas of any two of the three islands; complications could conceivably arise from differences in season of sampling, year of sampling, ratio of permanent and semi-permanent to temporary waters and number of localities sampled. However, it is important to note that in Australasia, calanoid copepods are nearly always present perennially in permanent standing waters (a few glacial or high altitude lakes are the only exceptions) despite wide fluctuations in population density (Bayly & Williams 1973). In any large sample at least some males and egg - or spermatophore-bearing females are present and the species determinable. This means that yearly or seasonal differences in sampling dates should not unduly influence the assessment of the fauna of the permanent waters. This leaves a residuum of problems for comparisons which, however, are not so great as to preclude the examination of a number of general features and trends.

The much cited island biogeography theory of

MacArthur & Wilson (1967) would predict that a positive correlation should exist between the number of species found within a discrete area and the size of that area. With respect to non-marine calanoids in the Australasian region, Table 4 indicates that across the whole spectrum of six land masses there is only a very rough correlation of the sort predicted. Several anomalies call for consideration and explanation.

King Island and Flinders Island differ only slightly in area but the former apparently has less than half the number of species found on the latter. This difference, if it is not an artefact, is difficult to explain but it may be significant that native habitat destruction, including the removal of vegetation, has proceeded to a greater extent on King Island than Flinders Island.

Kangaroo Island is about three and a half times larger than Flinders Island but has fewer calanoids (if the halobiont species *C. clitellata* is omitted it has only four species). It is difficult nowadays to find a large natural body of fresh water on Kangaroo Island. Extensive vegetation removal in the period 1945 - 1955 and the consequent rise in water tables and mobilisation of salt has resulted in the salinisation of several lowland lakes that were formerly fresh. Murray Lagoon originally contained fresh water but today it is saline (salinity 9.1 g l^{-1} on 3 July 1994; Table 1). Several of the lakes on Kangaroo Island visited during the winter of 1994 were found to be highly saline and were not sampled for that reason. Half of the natural fresh waters that were located were very small and temporary in character. It is conceivable that species like *Calamoecia gibbosa* and *C. tasmanica*, which occur in south-eastern and south-western Australia and typically inhabit permanent fresh waters, no longer occur on Kangaroo Island as a result of recent salinisation.

New Zealand is about four times larger than Tasmania but has fewer calanoids. However, during the Oligocene, some two-thirds of the area of modern New Zealand was covered by sea (Stevens 1980).

Boeckella symmetrica, which occurred on all three islands, and *B. triarticulata*, which was found on Kangaroo and Flinders Islands, are both common and widely distributed species (Bayly 1992a). The occurrence of *B. propinqua* on Flinders Island only (Table 3) is consistent with the existing evidence that, within Australia, this species is restricted to the far eastern fringe of the continent, previous Australian records are from the east coast of Tasmania and coastal New South Wales. *B. major* (Kangaroo and Flinders Islands; Tables 1 and 3) is characteristic of temporary waters and has been recorded previously from New South Wales, Victoria and Tasmania (Bayly 1992a). The present record from Kangaroo Island is the first from South Australian territory but it is likely that this merely reflects a lack of investigation in this State of the copepods of temporary ponds and pools. *B. pseudochelae* (King Island; Table 2) is another temporary water specialist previously noted from southern New South Wales, Victoria and Tasmania. *Calamoecia tasmanica* (King and Flinders Islands) and *C. ampulla* (Kangaroo Island) are widely distributed species known from south-eastern and south-western Australia (Bayly 1992a).

Hemiboeckella searli typically occurs in temporary ponds and pools, but, as with the present record from Flinders Island (Table 3), it also occurs in littoral weed beds in permanent or semi-permanent waters. This commonality of occurrence is not as incongruous as it first appears. Water permeating dense vegetation in the littoral region of a permanent lake has an ecological similarity to that in a shallow, temporary pool (including those entirely devoid of vegetation) that is not commonly appreciated namely the exclusion of predators. It is well appreciated that, in a newly formed pool, flying insect predators such as notonectids may take some time to arrive and, until this occurs, the habitat may be largely predator-free. The fact that *Hemiboeckella* characteristically occurs very early in pool successions (Bayly 1992b) suggests a high degree of predator susceptibility. However, as pointed out by Connell (1975) some prey species have evolved the ability to live in refuges that the predator cannot invade because *the habitat structure is too difficult to search*. It is presumably for this reason that dense littoral vegetation offers *H. searli* a refuge from limnetic fish and insect predators in lakes. *H. searli* is widely distributed, occurring in south-eastern and south-western Australia.

Calamoecia gibbosa has the most intriguing distribution of all the Australian freshwater calanoids; it occurs in Tasmania, on Flinders Island, along the coastal fringe of south-eastern South Australia between Mt Gambier and Salt Creek and on two granite outcrops near Balladonia in Western Australia (Bayly 1984, 1992a). A previously unpublished record is from near Mt Rough to the south-east of Salt Creek in South Australia. The two Western Australian populations were treated (Bayly 1979, 1992a) as belonging to a separate subspecies from the eastern form.

TABLE 4. *Land area and species richness*

Name of land mass	Area (km^2)	Number of calanoid species[a]
King Island	1,200	3
Flinders Island	1,330	7
Kangaroo Island	4,400	5
Tasmania	67,800	15
New Zealand	269,000	10
Australia	7,682,000	33

a. Belonging to the family Centropagidae and restricted to the genera *Boeckella*, *Hemiboeckella* and *Calamoecia*.

The most reasonable explanation for current disjunctions in the distribution of *C. gibbosa* is that, at the time of one of the three glacial maxima during the Late Pleistocene (Chappell 1978), probably the last one at 18 ka B.P., it was continuously distributed along a coastal lowland plain to the south of the present southern coastline of Australia. It may be supposed to have extended from eastern Bass Strait to the western limit of the Great Australian Bight (cf. Nelson 1981, fig. 2). A subsequent rise in sea level of more than 100 m (Chappell 1978) would then have been responsible for the present day disjunctions. The morphological evidence suggests that the Western Australian form is a derived rather than ancestral form. Thus it is proposed that, some time within the Wisconsin glaciation when sea levels had been lowered by about 100 m, gradual east to west dispersal of *C. gibbosa* occurred along a broad coastal plain that is now submerged. This proposal of east to west dispersal, followed by subspeciation in the west as a result of vicariant isolation, parallels the pattern of speciation in Western Australian frogs first proposed by Main *et al.* (1958) and subsequently adopted by Main (1968) and Littlejohn (1981). It should be noted, however, that more recent molecular data on frogs is said not to support multiple east to west invasions during the Pleistocene as being the explanation for speciation in Western Australia (Roberts & Maxson 1985).

If we accept submergence of the southern plain as the explanation for the disjunctions in the distribution of *C. gibbosa*, then three explanations may be offered for the apparent absence of this species from Kangaroo Island and King Island. First, the species does occur on these islands but the present samplings were not intensive enough to reveal it. Second, *C. gibbosa* was originally present on these islands but subsequent ecological changes (e.g. salinisation on Kangaroo Island) have brought about its local extinction. Third, although the original distribution of *C gibbosa* along the now submerged plain was continuous in a broad sense, it was nevertheless somewhat patchy, and the persistent land samples provided by these two islands were not sufficiently large to include this calanoid.

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